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Contents

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A COMPARATIVE STUDY OF THE ATLANTIC SALMON, *SALMO SALAR* LINNAEUS, AND THE LAKE SALMON, *SALMO SALAR SEBAGO* (GIRARD)[1]

BY D. G. WILDER[2]

Abstract

Twenty-six body measurements and counts were made on the majority of 381 specimens of lake and Atlantic salmon. Adult lake and Atlantic salmon generally differ in coloration, spotting, and flesh color. Evidence is presented that indicates that these differences are not inherent but result from differences in the environment and diet. In the parr and in the spawning adult stages no consistent differences in body measurements could be demonstrated. Non-spawning adult lake salmon tend to have larger head parts and longer fins than fresh-run Atlantic salmon grilse. These differences are associated with a slower growth rate, maturation at smaller sizes, and a more pronounced retention of the secondary sexual characteristics in the lake salmon. The average counts for certain meristic structures tend to increase with increase in length. When lake and Atlantic salmon of approximately the same size were compared no consistent differences in these meristic characters could be demonstrated. Lake and Atlantic salmon may be inherently different with respect to migratory behavior but the evidence available to date fails to establish such a difference.

Introduction

Certain lakes in eastern Canada and in the northeastern part of the United States support populations of fish that are usually referred to as landlocked, lake, or sebago salmon. In the Lake St. John region of Quebec, the corresponding fish is known as the ouananiche. The close affinity of these fish to the Atlantic salmon (*Salmo salar*) has long been recognized but their exact systematic status has been a question of much discussion and speculation.

The lake salmon was first described by Girard (1) who distinguished it from the Atlantic salmon on the basis of general shape, head size, and spotting. Although his description was apparently based on only two specimens from Sebago Lake, Maine, he believed the fish to be sufficiently distinct to warrant the specific name *Salmo sebago*. Jordan and Evermann (3) considered both the sebago salmon and the ouananiche of Quebec to be subspecies of the Atlantic salmon listing them, respectively, as *Salmo salar sebago* and *Salmo*

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salar ouananiche.   Kendall (4), however, felt that the lake salmon was distinct from the Atlantic salmon and restored the specific name of *Salmo sebago.*

The most striking way in which lake salmon differ from Atlantic salmon is that they fail to migrate to salt water even though in most cases they are not truly landlocked or prevented from descending to the sea by any physical barrier.   In addition to this behavior difference various workers have pointed out differences in size attained, in coloration, and in body proportions.   In the present study several populations of lake and Atlantic salmon have been compared and an attempt has been made to evaluate the observed differences in the light of known environmental effects.

I wish to express my appreciation to Prof. J. R. Dymond who suggested this problem and under whose supervision the work was carried out. Numerous suggestions by Dr. A. G. Huntsman and Mr. H. C. White proved extremely helpful.

Specimens Available for Study

The summer of 1939 was spent at Grand (Shubenacadie) Lake, N.S., which supports a population of lake salmon.   The Fish Culture Branch of the Department of Fisheries operates a rearing station for these lake salmon at the head of the lake.   Specimens of these rearing pond fish were collected and examined throughout the summer, salmon parr were seined from several rivers in the vicinity, and some adult lake salmon were obtained from Grand Lake.   During the summers of 1941 and 1942 observations were made on the Atlantic salmon of Moser River, Halifax Co., N.S.

In addition to the specimens obtained in the field the lake and sea salmon in the collection of the Royal Ontario Museum of Zoology were examined. Unfortunately the purity of the lake stocks is open to serious question. Extensive fish culture operations have been carried on in connection with the lake salmon and in the past both Grand Lake, N.S., and Chamcook Lake, N.B., or their tributary waters have been heavily stocked with young Atlantic salmon.   At Grand Lake, however, all fish have free access to the sea through the Shubenacadie River and the rearing pond stock is obtained from wild adult fish that have voluntarily remained in the lake.   At Chamcook Lake, of recent years at least, the migration of planted stock to or from the sea is prevented by an iron fence closing the outlet.   Some of the Chamcook specimens, particularly those collected in 1938, may well be the progeny of Atlantic salmon parents.   The locality, the number of specimens examined, and their condition at the time of capture are indicated in the following list.

Lake salmon

   Grand Lake, N.S.

      68 ♂, 84 ♀ :—Yearling parr to adults reared entirely in artificial ponds. Collected from June to August 1939.   Larger fish mature but not ripe when collected.

      2 ♂, 9 ♀ :—Three-year-old rearing pond stock released in spring of 1939, recaptured June 15 to July 6, 1939, immature.

    3♂, 6♀ :—Adult wild stock, obtained from anglers' catches from June to August 1939, not ripe.

    5♂, 5♀ :—Spent wild stock adults, stripped for hatchery purposes during November 1939, killed for examination Feb. 2, 1940.

    1♂, 6♀ :—Adult ouananiche four years old. Eggs obtained from Lake St. John, Que., and reared in Grand Lake rearing ponds. Collected June 21 to Aug. 24, 1939, not ripe.

Rawdon River, N.S.

    21♂, 4♀ :—Yearling and two-year old parr seined Sept. 9 to 18, 1939. Majority of males maturing.

Beaver River, N.S.

    7♂, 2♀ :—Yearling and two-year old parr, seined Sept. 9, 1939.

Chamcook Lake, N.B.

    8♂, 4♀ :—Yearling parr collected May 20, 1925.

    14♂, 8♀ :—Spent adults collected May 20, 1925.

    8♂, 4♀ :—Ripe adults collected Nov. 16, 1938.

Lake St. John, Que.

    3♂, 2♀ :—Ripening adults collected Sept. 21, 1927.

Atlantic salmon

Benery brook, N.S.

    8♂, 8♀ :—Yearling parr collected Aug. 11, 1939. Some of larger males maturing.

Sackville River, N.S.

    10♂, 7♀ :—Yearling and two-year-old parr collected Sept. 6, 1939. Larger males maturing.

Smith brook, N.S.

    11♂, 8♀ :—Yearling, two-year-old, and three-year-old parr collected July 22, 1939.

S. W. Margaree, N.S.

    9 not sexed:—Yearling and two-year-old parr. Collected July 31, 1936.

Mersey River, N.S.

    5♂, 4♀ :—Smolts collected May 15, 1931.

Salmon Lake, Que.

    4 not sexed:—Atlantic salmon planted October 1936, collected Sept. 6, 1938.

Moser River, N.S.

    5♂, 4♀ :—Fresh-run grilse collected July 11 to Aug. 7, 1941.

    6 not sexed:—Large fresh-run salmon collected June 12 to July 3, 1941.

Blanc Sablon River, Que.

    2♂, 5♀ :—Partially mended grilse kelts, spawned during fall of 1938, collected May 1 to June 8, 1939.

St. John River, N.B.

5 ♂:—Fresh-run grilse collected June to July 1934.

1 ♀ :—Large spawning salmon collected Nov. 5, 1932.

Sackville River, N.S.

1 ♂, 1 ♀ :—Spent grilse, collected Nov. 6, 1939.

Southampton River, N.B.

3 ♀ :—Large spawning salmon collected November 1934.

Methods

Many of the specimens collected during the summer of 1939 were examined shortly after collection while still in fresh condition. The remainder were preserved in 5% formalin and examined during the winter of 1939-40. Since the museum specimens collected from 1925 to 1939 varied considerably in their state of preservation when examined in 1939, no attempt has been made to correct for the effect of preservation. Such measurements as body depth, body width, and eye diameter are particularly unreliable in specimens that have been preserved for a long time.

The various characters that were measured or counted are indicated below. Abbreviations that are used elsewhere in this paper are shown in parentheses. All measurements and counts were made on the left side of the fish, the measurements being recorded to the nearest millimetre.

Standard length (SL) was measured from the tip of the snout to the end of the vertebral column.

Head length (HL) was measured from the tip of the snout to the most posterior part of the operculum, exclusive of the opercular membrane.

Head depth (HD) was measured from the base of the occiput to the most ventral portion of the operculum.

Maxillary (Max) was measured from the tip of the snout to the posterior end of the maxillary.

Snout (Sn) was measured from the tip of the snout to the anterior border of the eyeball.

Interorbital (I) was measured from the mid-point of one supraorbital process to that of the opposite side.

Eye (E) is the anteroposterior diameter of the eyeball.

Body depth (BD) is the greatest body depth.

Body width (BW) is the greatest body width.

Caudal peduncle length (CPL) is the horizontal distance from a vertical line passing through the posterior insertion of the anal fin to the end of the vertebral column.

Caudal peduncle depth (CPD) is the least depth of the caudal peduncle.

Dorsal height (DH) and anal height (AH) were measured along the longest fin ray with the fin extended.

Dorsal base (DB) and anal base (AB) were measured along the body from the anterior insertion to the posterior insertion.

Pectoral length (PL), ventral length (VL), and adipose (A) were measured from the anterior insertion to the posterior tip.

Dorsal and anal fin rays are the total number of developed rays, including divided and undivided rays. One or two undeveloped rays normally present were omitted when calculating averages.

Pectoral and ventral fin rays are the total number of rays, including undeveloped rays if present.

Branchiostegals, pyloric caeca, and gill rakers are total counts, the raker count being made on the first gill arch.

Scale rows were counted along the lateral line from the posterior margin of the head to the end of the vertebral column.

Coloration

The general color pattern and the size and number of black spots are characteristics that are usually stressed in distinguishing lake and Atlantic salmon. The following descriptions are based on observations made in the field on fresh specimens.

During the summer months adult Grand Lake salmon are usually dark green on the dorsal surface of the head and body but variations from olive green to almost black are common. This greenish color fades towards the lateral line, the sides being a light silvery gray and the belly in most cases white. The pectoral fins are usually dark gray but may be tinged with yellow or olive green. The ventral and anal fins are usually lighter than the pectorals and in some cases are tinged with yellow. The caudal fin is almost invariably a dark uniform gray.

The majority of the lake salmon have from three to eight circular black or brown spots up to $\frac{1}{4}$ in. in diameter on the upper half of the operculum and cheek, but as many as 19 of these spots have been counted and in rare cases they are completely lacking. Posterior to the head the spots are smaller but more numerous extending below the lateral line on the anterior portion of the body. Usually there are 25 to 75 black spots above the lateral line and 10 to 25 below but in some specimens they are too numerous and indistinct to estimate while in others they are completely lacking. The dorsal fin that is the only spotted fin commonly has 10 to 20 black spots but in rare cases it is immaculate.

In the spawning season the lake salmon develop a pinkish band about $\frac{1}{2}$ in. wide that extends along the lower side from the head to the base of the caudal fin. The pectoral, ventral, and anal fins, the outer branchiostegals and the posterior portion of the mandible also become tinged with this color. The posterior portion of the maxillary and the ventral half of the cheek and opercle usually turn a golden yellow while the caudal fin often becomes reddish brown. No sexual differences could be detected in this spawning coloration.

Atlantic salmon when caught in the sea are similar in color pattern to lake salmon but tend to be lighter in color, more silvery, and less heavily spotted. When they enter the rivers the blue green color of the dorsal surface quickly fades to a uniform gray. The sides of the head and body are very silvery and lightly spotted with small, often x-shaped black marks. The belly is white and the fins usually gray. These fish become darker as they remain in fresh water, the dorsal surface becoming almost black and the sides and belly turning gray. Individuals that have spent several months in the river are often referred to as 'black' salmon. Atlantic salmon kelts captured by H. C. White in the early spring of 1942 and retained in a small freshwater pond were very dark when examined by the writer during June and July. These fish had developed the numerous large black or brown spots on the head and body that are generally considered to be characteristic of lake salmon. Mr. White and the writer agreed that in general appearance these fish resembled lake salmon more closely than they did Atlantic salmon.

It is concluded from the above observations that the differences in coloration and marking commonly used to distinguish lake and Atlantic salmon are environmental effects and do not represent hereditary differences in the two groups of fish.

Flesh color

Atlantic salmon parr and smolts invariably have white or pale yellow flesh but in the sea the typical 'salmon-pink' flesh color is developed and the fresh-run grilse and larger salmon almost invariably have pink flesh. The lake salmon, however, retain the white or pale yellow flesh throughout life. This difference in flesh color has often been cited as proof of the distinctness of the two stocks.

The Atlantic salmon kelts retained by Mr. White (see above) were fed almost entirely on fresh gaspereaux (*Pomolobus pseudoharengus*) until their weight–length relationship equalled that of fresh-run salmon. These fish when examined by the writer during June and July were found to have white or pale yellow flesh.

Although it has not been demonstrated that lake salmon are capable of developing pink flesh it is believed that in both lake and Atlantic salmon the flesh color is dependent on diet.

Measurements

In comparing measurements of several samples of salmonid fish certain difficulties arise. Mottley (5) has shown that in Kamloops trout several characters grow at rates that differ from that of the fish as a whole. The eye, for example, throughout the size range studied grows at a much slower rate than the body with the result that large trout have relatively small eyes. Mottley has shown further that the relative growth rates of several characters are not constant throughout life. At the onset of sexual maturity such structures as the head, snout and maxillary, which have been growing at a relatively slower rate than the body, begin to grow at a relatively faster rate.

These observations have been confirmed by the writer for both the Atlantic salmon and for the speckled trout (*Salvelinus fontinalis*). White (6) has shown that slow growing Atlantic salmon parr tend to have larger heads and eyes than fast growing fish of the same size. In a homogeneous stock of speckled trout the writer (7) has demonstrated marked differences in the relative sizes of various body parts of trout reared from fertilization to hatching at different temperatures.

These differences in the relative sizes of body characters associated with absolute size, sexual maturity, rate of growth, and developmental temperatures render the assessment of differences in various stocks of salmon extremely difficult. To demonstrate inherent characteristics, the different stocks should be reared under identical conditions and specimens of the same size, age, sex, and state of maturity compared. This procedure, however, is not usually possible and in the present study an attempt has been made to evaluate the observed differences in the light of these environmental effects.

The various samples available for study are made up of fish that vary considerably in size range, state of sexual maturity, and in growth rate. Some of the samples are composed entirely of parr, other samples include only adult lake salmon, and others are made up of grilse and larger Atlantic salmon. Fortunately, however, a rather complete series of nonspawning Grand Lake fish ranging from 6 to 47 cm. in length is available and has been used as a standard for comparison with the other samples. The data for these Grand Lake fish were sorted according to length and sex and the average values shown in Table I calculated for each group of 10 fish. For the other samples in which the specimens extended over a sufficiently wide length range the individual measurements of each character were plotted against standard length on double logarithmic paper. Straight lines were fitted to these points by inspection and the size of each character corresponding to the average standard length of the sample was determined by interpolation. The grilse from the Moser, the Blanc Sablon, and the Saint John Rivers and the four Atlantic salmon from Salmon Lake extended over too short a length range to permit this method of analysis. With these four samples simple arithmetic averages were calculated. The values calculated for all samples other than the nonspawning Grand Lake fish are shown in Tables II and III. Many of the lake and Atlantic salmon male parr were maturing when collected during August and September but since no effect of this approaching maturity on the relative sizes of the body parts could be detected the sexes of the parr have not been considered separately.

Some of the male Atlantic salmon mature as parr at a standard length of 10 to 18 cm. After descending to the sea as smolts, these salmon grow at a much faster rate than the lake salmon, returning to the rivers about one year later as grilse at a standard length of 45 to 50 cm. The male lake salmon also mature as parr and the females start spawning at a standard length of about 25 cm. so that the both sexes spawn several times before they reach the size of Atlantic salmon grilse. This maturity at smaller sizes, associated with a

TABLE I

Average sizes of body parts of nonspawning Grand Lake salmon. Groups of 10 fish, all measurements in millimetres

	SL	HL	HD	Max	Sn	I	E	D	W	CPL	CPD	DH	DB	A	AH	AB	PL	VL
Males	84	21.8	12.3	10.0	5.9	6.3	6.2	18.6	12.2	14.0	7.7	13.8	12.0	6.4	11.1	7.0	17.9	12.8
	121	30.9	17.6	14.7	8.5	8.5	7.9	28.0	17.2	20.9	10.8	18.4	17.5	7.8	15.3	10.4	23.4	16.7
	160	38.7	22.3	17.6	10.1	11.5	9.4	33.5	20.8	28.0	12.5	20.3	21.1	9.8	16.4	12.7	26.8	19.1
	178	43.5	24.6	19.8	12.2	11.6	10.3	36.6	21.0	31.6	13.9	21.5	24.7	10.9	17.2	15.5	29.6	20.9
	191	46.3	26.6	22.0	12.7	13.0	10.5	40.9	23.8	34.8	15.1	22.8	25.7	11.9	18.7	15.3	31.2	22.6
	233	58.8	33.4	30.8	19.2	18.1	12.1	49.4	31.0	38.5	19.9	32.3	33.6	16.3	26.4	22.1	41.3	31.2
	288	70.0	40.8	35.1	22.1	23.2	14.0	61.9	39.2	49.3	23.4	34.8	38.8	19.4	30.7	25.3	46.9	33.8
	379*	89	51	49	31	28	17	70	44	68	27	44	50	27	37	36	57	44
Females	93	24.0	13.8	10.8	6.1	6.4	6.7	21.2	12.8	15.3	8.3	13.7	13.4	6.1	11.5	7.8	18.3	13.5
	128	32.5	18.2	15.1	8.9	8.8	8.3	26.8	16.9	22.0	10.7	19.1	18.8	7.9	15.6	10.8	24.1	17.8
	165	39.5	22.6	18.2	10.5	11.0	9.5	34.4	21.0	29.6	13.0	21.9	22.6	10.2	16.4	13.2	27.3	19.7
	186	44.4	25.1	20.6	12.1	12.3	10.4	37.6	22.7	33.0	14.7	22.2	25.7	11.0	18.4	15.6	29.9	21.6
	205	47.4	27.0	22.4	13.3	13.7	10.9	42.7	25.4	37.0	15.8	23.6	27.2	12.8	18.8	16.8	31.6	22.9
	248	56.6	33.4	27.0	15.9	17.5	12.6	50.9	31.8	43.7	20.0	28.3	33.5	16.2	24.3	21.9	38.9	29.0
	281	62.1	38.3	29.6	17.4	20.1	13.6	58.7	35.9	50.2	22.3	32.1	38.0	18.2	27.2	25.5	42.9	31.0
	302	66.2	40.0	32.1	19.2	21.4	14.3	60.3	38.1	55.2	23.5	33.7	38.6	19.5	28.2	26.3	44.5	32.3
	393	87.1	51.5	43.1	27.1	29.3	16.7	75.5	47.0	69.0	30.2	40.6	49.8	23.8	36.0	36.2	54.1	40.4

* One specimen only.

TABLE II

AVERAGE SIZES OF BODY PARTS OF LAKE SALMON. ALL MEASUREMENTS IN MILLIMETRES

	Sex	n	SL	HL	HD	Max	Sn	I	E	D	W	CPL	CPD	DH	DB	A	AH	AB	PL	VL
Chamcook Lake 1925	♂ and ♀	12	97	26	14	11	6.5	8.0	6.1	21	14	16	8.6	15	14	6.8	11	8.7	19	13
Beaver River	♂ and ♀	9	117	33	18	15	9.0	8.0	8.0	26	18	18	11	17	17	7.4	13	11	24	16
Rawdon River	♂ and ♀	25	132	32	19	15	9.2	9.1	7.8	29	19	22	12	20	18	8.7	14	12	25	17
Grand Lake planted stock	♂ and ♀	11	245	57	33	27	16	18	13	44	26	45	18	31	32	—	24	20	39	29
" " wild stock	♂	5	348	89	50	46	31	32	14	69	49	51	30	42	44	26	33	32	51	39
" " wild stock	♀	5	364	86	51	42	26	30	15	67	46	55	30	42	48	20	33	35	51	38
Chamcook Lake 1925	♂	14	380	91	53	44	27	32	13	90	41	63	33	50	49	24	39	34	58	44
" " 1925	♀	8	372	87	50	42	24	31	13	87	40	63	33	47	46	23	37	32	56	42
" " 1938	♂	8	263	68	36	34	22	22	12	54	29	41	23	38	36	19	30	24	47	35
" " 1938	♂	4	462	104	60	53	34	36	17	88	48	76	38	56	61	30	45	43	68	51
Lake St. John	♂	4	417	104	60	53	33	37	17	94	44	68	35	55	53	22	48	38	73	56
"	♀	8	339	80	47	41	24	26	16	79	47	53	29	45	47	—	39	33	56	44

TABLE III

AVERAGE SIZES OF BODY PARTS OF ATLANTIC SALMON.   ALL MEASUREMENTS IN MILLIMETRES

	Sex	n	SL	HL	HD	Max	Sn	I	E	D	W	CPL	CPD	DH	DB	A	AH	AB	PL	VL
Benery brook	♂ and ♀	16	92	24	14	11	6.2	6.0	6.7	20	14	15	8.8	14	12	7.0	11	7.5	20	13
Sackville River	♂ and ♀	17	103	27	15	12	7.0	6.4	7.4	22	15	17	9.3	16	14	7.3	12	9.6	22	15
Smith brook	♂ and ♀	19	110	28	17	13	7.6	6.8	7.6	25	18	17	11	17	16	8.4	13	10	24	16
S.W. Margaree River	?	9	131	31	19	13	8.2	8.7	7.5	32	23	22	13	17	20	9.6	14	13	23	16
Mersey River	♂ and ♀	9	204	47	26	20	10	14	10	41	21	38	17	28	23	11	22	17	35	25
Salmon Lake	?	4	316	64	30	35	18	22	12	60	39	60	24	34	36	18	29	24	44	32
Moser River	♂	5	478	100	58	49	34	37	17	107	59	86	37	50	58	29	45	40	65	49
" "	♀	4	472	90	54	44	30	34	15	102	59	—	37	48	59	29	42	42	59	46
Blanc Sablon River	♂	2	502	122	64	65	48	44	16	88	48	86	37	60	58	33	52	42	72	59
" "	♀	5	462	99	60	48	32	37	15	84	47	79	35	56	54	26	48	41	66	50
Saint John River	♂	5	497	110	60	54	35	40	16	103	53	87	37	59	62	29	50	42	66	53
Sackville River	♂	1	471	108	64	58	41	41	15	95	50	72	40	51	59	32	49	39	66	53
" "	♀	1	487	106	62	53	35	37	15	107	50	77	39	52	57	32	47	44	69	51

slow growth rate between successive spawnings, results in the development of secondary sexual characteristics in relatively small lake salmon and a more pronounced retention of these characteristics throughout nonbreeding periods. The greater development of the secondary sexual characteristics in non-spawning Grand Lake salmon as compared to fresh-run Atlantic salmon grilse is clearly shown by the following measurements, all of which are in millimetres.

	Standard length	Head length		% Diff.	Maxil-lary		% Diff.	Snout		% Diff.
		♂	♀		♂	♀		♂	♀	
Moser River fresh-run grilse	480	100	92	8.7	50	45	11.1	34	31	9.7
Grand Lake nonspawning adults	350	83	75	10.7	48	37	24.7	30	23	30.4

With the lake salmon maturing at smaller sizes and retaining the secondary sexual characteristics to a greater degree it is virtually impossible, beyond the parr and smolt stages, to obtain specimens of lake and Atlantic salmon of the same size that have these characteristics developed to the same degree. Since, however, the changes associated with maturity are much less marked in the female salmon, these have been used in the preparation of Fig. 1. In this figure the data for certain characters of nonspawning Grand Lake female salmon are represented by straight lines. The data for the other samples of lake salmon are indicated by open circles and for the Atlantic salmon by closed circles. The particular sample to which each circle refers may be determined by reference to the average standard lengths in Tables II and III.

It may be seen from an inspection of this figure that the lake and Atlantic salmon do not differ consistently in any one character. Fresh-run grilse from the Moser River tend to have smaller head parts and shorter fins than the nonspawning Grand Lake stock. The spent or spawning grilse from the Blanc Sablon and Sackville Rivers, however, have larger head parts and longer fins than the nonspawning Grand Lake fish but are very similar to spent or spawning lake salmon from Grand Lake and Chamcook Lake.

Kendall (4) concluded that the most salient difference between the lake salmon and the Atlantic salmon is in the ratio of caudal peduncle depth to caudal peduncle length, the Atlantic salmon beyond the parr stage having more slender caudal peduncles. The present data do not support this con-clusion since it may be seen in Fig. 1 that in the majority of cases the Atlantic salmon have caudal peduncles that are relatively shorter and deeper than the Grand Lake fish.

From the above data it is concluded that, in the parr stages, the lake salmon as a group do not differ significantly from the Atlantic salmon in any of the

characters measured. The differences commonly observed in comparing adult nonspawning lake and Atlantic salmon are believed to result from a differential development and retention of the secondary sexual characteristics, which are associated with a slower growth rate in the lake salmon.
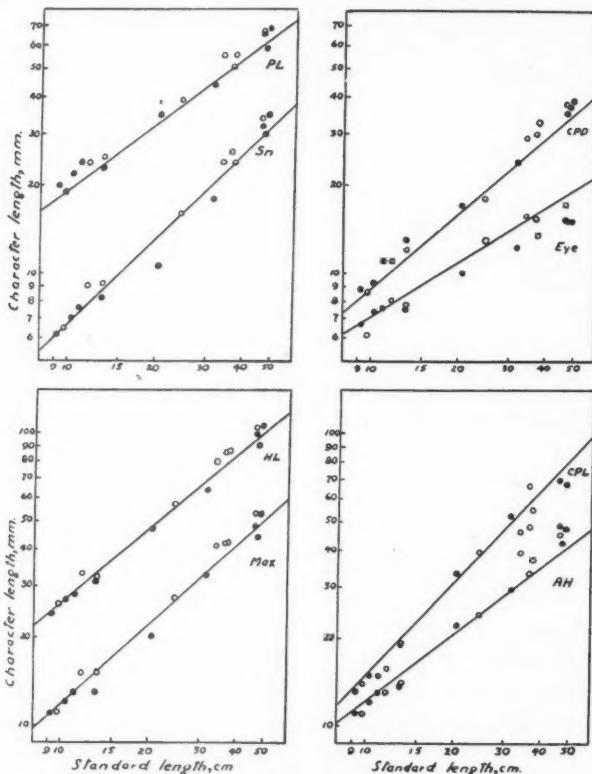
FIG. 1. *Relationship of character length and body length. Nonspawning Grand Lake salmon represented by straight lines, other samples of lake salmon by open circles, and Atlantic salmon by closed circles.*

Counts

Prior to comparing the average counts obtained for the various samples all the Grand Lake data were sorted according to size and sex. Since no sexual differences could be detected in these data, the sexes have been lumped in the following comparisons. The averages determined for the several size groups of Grand Lake salmon are indicated in Table IV where it is obvious that the average counts for certain characters tend to increase with size. This tendency when tested by the analysis of variance was found to be statistically significant (P less than .01) for all counts except the dorsal and anal fin rays. Because of this variation with size further comparisons have been restricted

TABLE IV

AVERAGE COUNTS FOR DIFFERENT SIZE GROUPS OF GRAND LAKE
SALMON, NUMBER OF SPECIMENS IN PARENTHESES

Size group, cm.	Scale rows	Gill rakers	Pyloric caeca	Branchiostegals	Pectoral rays	Dorsal rays	Anal rays
8-15	107.8 (16)	17.2 (26)	47.7 (7)	10.5 (28)	13.5 (39)	11.7 (39)	8.9 (42)
15-20	110.3 (35)	18.2 (35)	51.0 (20)	10.4 (51)	13.6 (45)	11.9 (29)	9.0 (51)
20-25	110.6 (19)	18.8 (22)	56.9 (21)	11.1 (25)	13.7 (25)	11.5 (19)	9.1 (25)
25-30	111.7 (32)	18.5 (32)	55.7 (32)	11.3 (33)	13.9 (33)	11.9 (22)	9.0 (33)
30 +	112.1 (27)	19.7 (29)	53.1 (28)	11.2 (28)	13.9 (29)	11.8 (25)	9.2 (29)

to samples of approximately the same average length. The 8 to 15 cm. group of Grand Lake salmon has been considered with the other samples of lake salmon parr and the 30 + cm. group with the other adult lake fish. The average values obtained for the parr and adult samples of both lake and Atlantic salmon are indicated in Tables V and VI. Since the ventral fin showed no variation in ray count, each specimen examined having a count of one undivided ray followed by eight divided rays, these data have not been included in the above tables.

TABLE V

AVERAGE COUNTS FOR SAMPLES OF LAKE AND ATLANTIC SALMON
PARR, NUMBER OF SPECIMENS IN PARENTHESES

Population	Scale rows	Gill rakers	Pyloric caeca	Branchiostegals	Pectoral rays	Dorsal rays	Anal rays
Lake salmon							
Grand Lake	107.8** (16)	17.2** (26)	47.7 (7)	10.5** (28)	13.5** (39)	11.7 (39)	8.9** (42)
Chamcook Lake	109.9** (12)	17.9 (11)		12.0** (12)	13.4** (12)	12.0 (12)	9.0 (12)
Rawdon River	112.6 (21)	18.4 (22)	52.3 (6)	11.2 (22)	13.8 (24)	11.6 (23)	8.9 (24)
Beaver River	112.0 (8)	18.1 (9)		11.9** (9)	13.9 (9)	12.4** (9)	8.9 (9)
All lake salmon parr	110.6* (57)	17.85* (68)	49.85 (13)	11.13 (71)	13.63** (84)	11.83 (83)	8.88** (87)
Atlantic salmon							
Benery brook	111.9 (15)	18.0 (16)		10.9 (16)	13.9 (16)	11.7 (16)	8.9 (15)
Sackville River	112.2 (17)	18.6 (17)		11.4 (15)	13.9 (17)	11.8 (17)	9.1 (17)
Smith brook	111.5 (18)	18.3 (19)		11.4 (19)	13.9 (19)	11.8 (19)	9.4 (19)
All Atlantic salmon parr	111.9 (50)	18.31 (52)		11.24 (50)	13.92 (52)	11.79 (52)	9.12 (51)

* Differs from average for all Atlantic salmon parr at 5% level of significance.
** Differs from average for all Atlantic salmon parr at 1% level of significance.

The average values for each sample of lake salmon have been compared with the over-all averages for the parr or adult Atlantic salmon, using the analysis of variance as a test of significance. Statistically significant differences are indicated in Tables V and VI by a single asterisk at the 5% level

TABLE VI

AVERAGE COUNTS FOR SAMPLES OF LAKE AND ATLANTIC SALMON
ADULTS, NUMBER OF SPECIMENS IN PARENTHESES

Population	Scale rows	Gill rakers	Pyloric caeca	Branchio-stegals	Pectoral rays	Dorsal rays	Anal rays
Lake salmon							
Grand Lake	112.1** (27)	19.7** (29)	53.1* (28)	11.2 (28)	13.9 (29)	11.8* (25)	9.2 (29)
Chamcook Lake 1925	114.1 (22)	20.2** (22)	58.7 (6)	11.9**(22)	14.2 (22)	12.1** (22)	9.3 (22)
Chamcook Lake 1938	111.5** (12)	18.8 (12)	62.0* (8)	11.6 (12)	13.8 (12)	11.9* (10)	9.1 (12)
Lake St. John	114.0 (11)	19.1 (11)	63.3** (11)	11.2 (11)	14.4* (12)	11.7 (12)	9.6* (12)
All lake salmon	112.9** (72)	19.59**(74)	57.23 (53)	11.48 (73)	14.05 (75)	11.87**(69)	9.25 (75)
Atlantic salmon							
Salmon Lake	118.2 (4)	19 (1)		10.5 (4)	13.5 (4)	11.2 (4)	9.5 (4)
Moser River	117.1 (10)	18.3 (9)	55.0 (3)	11.3 (14)	13.9 (14)	11.6 (14)	9.1 (14)
Blanc Sablon River	111.3 (7)	19.3 (7)	60.6 (7)	11.6 (7)	13.9 (7)	11.1 (7)	8.7 (7)
Saint John River	117.5 (6)	19.0 (6)		11.0 (5)	14.2 (6)	11.2 (6)	9.2 (4)
Sackville River	113.0 (2)	19.0 (2)	55.0 (2)	11.0 (2)	14.0 (2)	12.0 (2)	9.5 (2)
Southampton River	114.7 (3)	18.3 (3)	53.3 (3)	11.3 (3)	14.3 (3)	11.7 (3)	9.0 (3)
All Atlantic salmon	115.6 (32)	18.78 (28)	57.27 (15)	11.20 (35)	13.94 (36)	11.42 (36)	9.09 (34)

* *Differs from average for all Atlantic salmon adults at 5% level of significance.*
** *Differs from average for all Atlantic salmon adults at 1% level of significance.*

of significance and by a double asterisk at the 1% level. In no case do the sample averages for lake salmon and the over-all averages for Atlantic salmon differ consistently. For each of the characters studied some samples of lake salmon averaged significantly lower than the Atlantic salmon whereas other samples either averaged higher or showed no significant differences. From these observations it is concluded that lake salmon as a group do not differ inherently from the Atlantic salmon in any of the meristic characters studied.

Migratory Behavior

Although nonspawning adult lake salmon generally differ from fresh-run Atlantic salmon grilse in having larger head parts, longer fins, and more numerous, larger spots these differences do not occur in the parr stages and it is believed that these are not inherent characteristics but result from environmental differences. There is, however, the possibility that lake and Atlantic salmon are inherently different with respect to migratory behavior. This possibility is being investigated by A. G. Huntsman at Grand Lake, N.S., where yearling lake and Atlantic salmon were planted together in June 1944 and 1945. To date (Huntsman (2)) it has not been possible to demonstrate any differences in the migratory behavior of these planted fish.

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THE GENETICS OF THE COLOUR PHASES OF THE RED FOX IN THE MACKENZIE RIVER LOCALITY[1]

By L. Butler[2]

Abstract

The red fox (*Vulpes fulva*) exists in the wild in three coat colour phases; red, cross, and silver or black. These three phases result from the action of one pair of alleles, the homozygotes being silver and red and the heterozygote being cross. At least two different mutations have occurred giving rise to the Canadian gene in eastern Canada and the Alaskan gene in western Canada. The mixing of these two mutant genes complicates the gene frequency analysis.

The proportions of the three colour phases are shown to vary with (1) locality, (2) state of population cycle, (3) population trend, (4) migration pressure. Of these factors the variations with locality and population trend are fairly satisfactorily explained by selection but the fluctuation of colour phase proportions with the population cycle is not. On the other hand all the facts can be explained by a migration theory, with or without selection. By migration, a mixture of native and migrant populations with different gene frequencies is obtained. Such migrations tend to be rhythmic since they are connected with the population cycle. In the year that migration took place the pelt returns reveal aberrant gene frequencies or colour phase ratios. In the following years the gene frequencies quickly approach equilibrium that may be at the premigration level or at a new one depending upon the success of the migrants in establishing themselves in the breeding population.

The marked diminution in the percentage silver and cross is due to the rapid population increase in an area of low frequency of the silver producing gene and the migration of this type into areas of higher frequency.

The red fox, *Vulpes fulva*, exists in three coat colour phases: silver, cross, and red. In a recent paper by Butler (2) the genetics and distribution of these colour phases across Canada were discussed, the data used for this purpose being the Hudson's Bay Company fur returns from 1915 to 1944. The gene frequency tests indicated that only in British Columbia were the ratios consistent with a single factor theory. Elsewhere they could be explained by the two factor hypothesis of Warwick and Hanson (1). The silver-producing allele *(a)* of the Alaskan factor is most abundant in the west and becomes decreasingly abundant in geographic progression as one moves eastward. The Canadian gene *(b)* has the opposite distribution. The data grouped in pentads by provinces revealed that the percentage silver had decreased steadily in most provinces. It was suggested that the reduction may be due to one or more of the following reasons:

1. The mixing of Canadian and Alaskan genes.

2. The northward migration of the southern type of fox with its lower frequency of silver-producing genes.

3. Selection against the silver type operating through differential fertility or survival of silver foxes in comparison to reds and crosses.

In order to throw more light on this subject the following paper deals with the fur returns of an isolated section for the periods 1860–1893 and 1915–1946.

The pelt data are collected chiefly from the Great Slave Lake region and the watersheds of the Mackenzie and its main tributary the Liard River (Figs. 1, 2). This country is bounded on the west by the Peel and Richardson
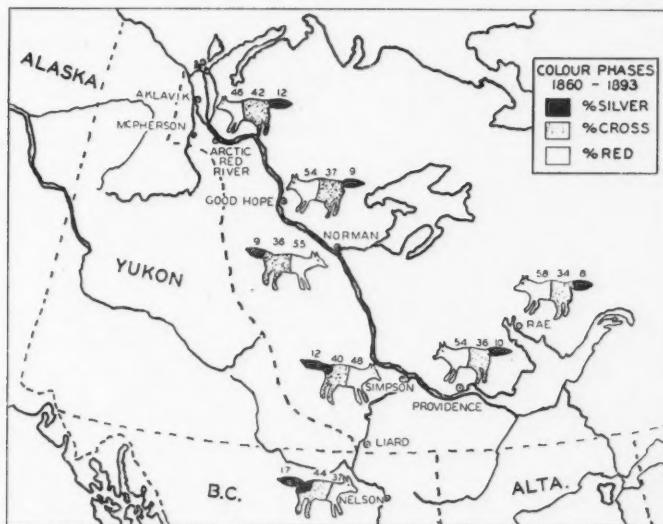

FIG. 1. *Geographic distribution of fox colour phases, 1860–1893.*

mountain ranges, on the north by the Beaufort Sea, and in the east by the Arctic tundra. Migration, if it takes place, is therefore fairly well restricted except from the south. The fox species of this region according to Seton is *V. alascensis* with *V. abietorum* in the south and with *V. fulvus* coming in at the S. E. border. It is perfectly feasible to theorize that if there has been enough isolation to develop different coat and skull characters there should also be different colour phase ratios, and that any periodic migrations would mix these in various proportions.

The Population Cycle

The yearly numbers of red fox are known to fluctuate rhythmically with high populations occurring over most of Canada every 8 to 10 years. Population cycles affect colour ratios (Butler (2, p. 48)) so population statistics are here presented for the information they may give on changes in gene frequency and possible migrational movements. The causes of the cycle may be food or weather factors as suggested by Elton *et al.*, or may arise from the interaction of environmental factors, but whatever their cause the solution of these genetic problems of populations leads us to consider them. Lack

of coincidence in peaks, or peaks occurring in one locality and not in adjacent ones, provide valuable clues to migration and the possible mixing of races with different gene frequencies.
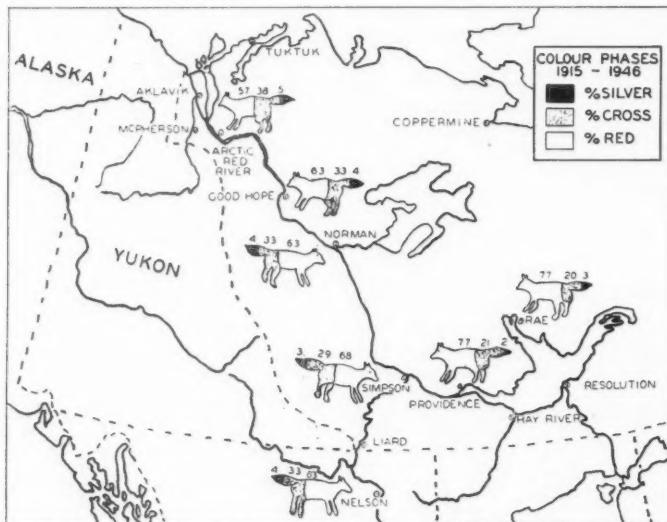
FIG. 2. *Geographic distribution of coat colours in Vulpes, 1915–46.*
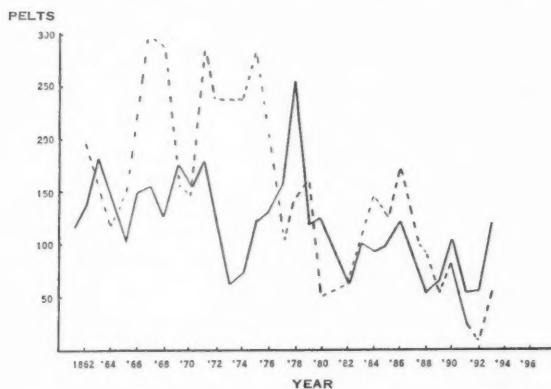
FIG. 3. *Total fox pelts taken each year at Forts Good Hope and Rae;* ———— *Good Hope,* - - - - *Fort Rae.*

The total number of fox pelts taken at two of the main collecting posts in the period 1860–1893 are plotted in Fig. 3. The data are plotted arithmetically to be consistent with the genetic data presented later. Examination of these early collection figures reveals no clear-cut 10-year cycle such as appears

in the 1915–1946 data presented in Figs. 5 to 8.   The chief characteristics of the collections are as follows.

Fort McPherson—violent fluctuations about a trend that increased up to 1875 and decreased thereafter.   The main fluctuations correspond to the
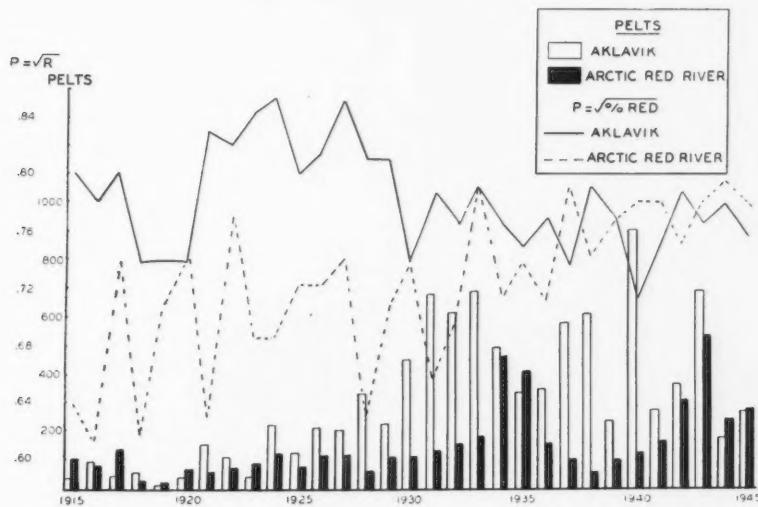
FIG. 4.   *Gene frequencies and population numbers, Aklavik and Arctic Red River.*
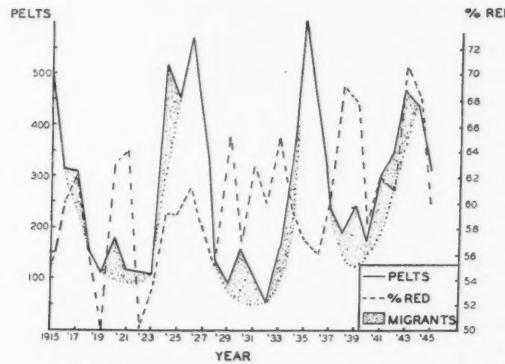
FIG. 5.   *Number of migrant foxes in relation to percentage red and total pelts, Forts Good Hope and Norman.*

Arctic type of cycle with four-year peaks, which is characteristic of the white fox population of the delta region.   In general, as can be seen below, the peak years of white and coloured fox coincide.

Fort Good Hope—a poorly defined 10-year cycle with some minor fluctuations that can be interpreted as being caused by the arctic cycle.

Fort Rae—a mixture of the arctic and 10-year cycle.
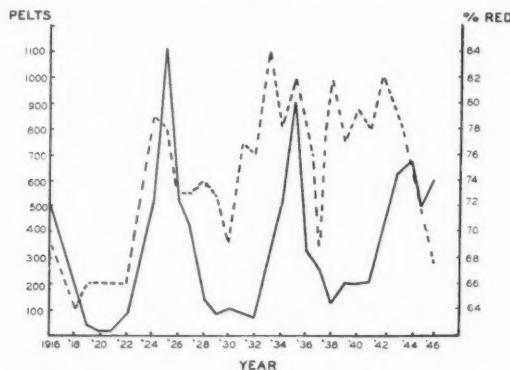
Fig. 6. *Total fox pelts taken and percentage of the red phase, Fort Providence and Hay River;* ——— *total pelts,* – – – – *% red.*
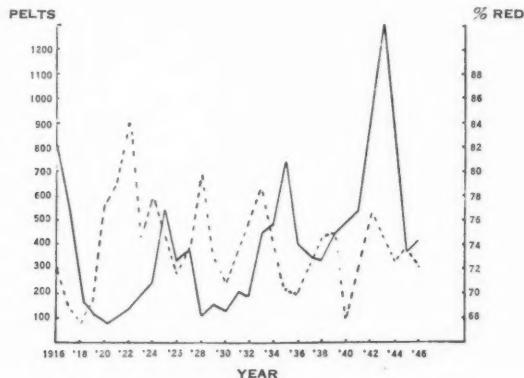
Fig. 7. *Total fox pelts taken and percentage of the red phase, Fort Resolution;* ——— *total pelts,* – – – *% red.*

The correspondence between peak years can be seen from the chart below.

PEAK YEARS

White Fox	1861		1864	*1868*		1872		1876	*1878*		1881	1884			*1887*
Ft. McPherson	*1861*		1864	1868	*1871*		*1875*		*1878*		*1881*		1885		
Ft. Rae				*1867–68*	*1871*		*1875*			1879				*1886*	
Ft. Good Hope		1863			1871				*1878*				1886	

The years shown in italics are the better defined peaks. The year 1871 was the only peak year at all points.

Turning next to the modern period, 1915–1946, we find that along with a general increase in numbers the pelt collections at Rae, Providence, and Good
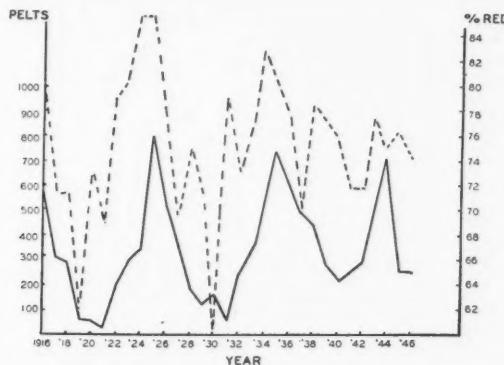


FIG. 8. *Total fox pelts taken and percentage of the red phase, Fort Rae; ——— total pelts,* – – – – *% red.*

Hope are definitely of the 10-year cycle type (Figs. 4 to 6) with peaks in 1925, 1935, and 1944. In the first two peaks, Good Hope lags behind Rae and Providence, which may indicate migration from the south. Three posts (McPherson, Aklavik, and Arctic Red River) draw from the area that was served by McPherson alone in the earlier period. McPherson and Arctic Red River are of the 10-year type of cycle while Aklavik, the most northerly post, is of the four-year arctic type of cycle. The combined data for all three posts illustrates how the population curves can be complicated by the use of heterogeneous data and indicates what may happen to gene frequency distributions from such regions.

Many sources of error are liable to occur in data such as these. In the first place, the use of pelt numbers as a criterion of population changes presupposes that the proportion trapped each year bears a definite relationship to the total available population. We have no statistical evidence on this point and some observations indicate that animals are easier to trap when they are plentiful and often trap-shy and wary when they are scarce; the percentage trapped in a peak population will be greater than in a low population. If this is so the pelt figures will still indicate the population ups and downs but will distort the magnitude. The effect of this possible error on the colour phase ratio should be negligible unless one colour phase is more easily trapped than the others. Another cause of error in the 1860 series is that the fur from some outposts did not always reach the parent post in the year that it was trapped and consequently it was included with the following year's fur.

These and other possible sources of error must be considered since we have no way of eliminating them from the 1860 data.

General Distribution of the Colour Phases

Although there are yearly fluctuations in the proportions of the different colour phases, a general picture of the regional distribution can be obtained at each post for the two periods. When this is done we get the following series, which are illustrated in Figs. 1 and 2:

	Silver		Cross	
	1860–93	1915–45	1860–93	1915–45
Fort McPherson	12.0	5.23	42.7	37.7
Fort Good Hope	8.6	4.10	37.4	33.3
Fort Norman	8.8	3.97	36.3	32.8
Fort Providence	9.7	2.03	35.8	21.0
Fort Rae	8.5	2.56	33.7	20.0

Examination of these figures in relation to the geography of the post (Fig. 1) shows cross fox in a perfect descending series from north to south in both periods. The percentage silver shows a similar descending series but it is not as regular as that for cross fox. Northern foxes have a much greater proportion of both silvers and crosses.

The other important point is the large decreases in the percentages of both silver and cross foxes at all posts when the 1860 series is compared with the 1915 one. There is a 6.0% (9.5 to 3.5) decrease in silvers and a 8.0% (37 to 29) decrease in cross. Although the north/south gradient is maintained the amount of decrease between the two series for each post is not uniform. Good Hope and Norman show the least decrease in both silvers and crosses. McPherson shows a large decrease in silvers and a small one in cross fox. Rae and Providence show large decreases in silver and very large decreases in cross. We can generalize by saying that in the north silvers have been decreasing relatively faster than crosses, while in the south the opposite situation prevails. Since these changes are due to a variety of causes no regression figures are given; each section will be discussed separately.

A curious difference between the 1860 and 1915 series is that when the percentage of red is plotted against the percentage of cross for each post, the co-ordinates of the 1860 series all lie below the curve of the theoretical value on a monofactorial basis, and the co-ordinates of the 1915 series all lie above this curve. Thus on a single factor basis the cross fox in the 1860 data are approximately 2% short of the expected whilst in the 1915 data they are 2% more than expected. To compensate for this the silver is higher than expected in the old series and lower than expected in the 1915 series. A possible explanation for the higher percentage of silvers in the early series lies in their greater value at that time. Trappers forced to travel great distances through

almost inaccessible country to market their furs would carry one silver pelt rather than the 10 or more reds required for equal value.   Also a few furs are utilized by the natives for parka trimmings, etc., and these would tend to be the cheaper reds rather than the silvers.

In the north/south series of five posts previously discussed, Fort Simpson, lying between Norman and Providence, was omitted on purpose.   This post lies at the junction of the Liard and Mackenzie Rivers and seems to be more influenced by the drift down the Liard than it is by the Mackenzie.   It appears to fit into the following series:

	Silver		Cross	
	1860–93	1915–45	1860–93	1915–45
Fort Simpson	12.0	2.93	39.6	28.9
Fort Liard	16.2	4.10	42.5	30.2
Fort Nelson	17.0	4.05	44.1	33.0

The percentage of both silver and cross increases as you move up the Liard River and into northern British Columbia.   Both the 1860 and the 1915 series show this trend very well although there has been a very large reduction in both the percentage silver and the percentage cross between the two series.

Population Genetics

We have already pointed out a number of differences between the colour phase ratios at the various posts.   In view of these differences it seems advisable to take each region separately in considering the distribution of coat colour genes.

Fort McPherson is situated in the delta of the Mackenzie and is the most northerly collecting centre in the 1860 series.   The distribution of colour phases collected by this post in the period 1860-93 was 12.0% silver, 42.7% cross, and 45.3% red.   Fitting this to a single factor scheme we get a P of .03, which indicates that the chances of a random deviation of this magnitude occurring are 3 in 100 samples of this size.   We have too many silver and too few crosses to satisfy the single factor scheme with these lumped data.   The two factor hypothesis used in the last paper does not fit the data any better, and in view of later evidence it seems unlikely that the Canadian gene b was in this area at such an early date.   Failure to obtain a fit by either method suggests that there may be large yearly fluctuations in population.   It would be better to work on a yearly basis, but numbers are so small during population lows that some grouping of data seems desirable.   To get a fairly homogeneous grouping of the yearly data the percentage of red was plotted.   Examination of this graph showed the first 10 years to be very erratic, the next 16 years showed chance fluctuations about a line of decreasing percentage of reds, and

the last seven years showed a sharp increase in the percentage of reds. Concomitant with this last increase in reds there was a decrease in the average yearly number of pelts from 334 to 95.

Dividing the series up in this manner and again testing for single factor inheritance we get the following χ^2 values:

$$
\begin{array}{ll}
1860-70\ldots\ldots & 33.7 \\
1871-86\ldots\ldots & .567 \\
1887-93\ldots\ldots & .37
\end{array}
$$

It appears that all ratios except the first 10 years are explainable by the single factor hypothesis. Testing the data for heterogeneity we find that the only group that is significantly heterogeneous is the first one. The χ^2 for heterogeneity for the 1860–70 values is 36.42 with nine degrees of freedom, a value that is highly significant. Looking over the first 10 years, we find that two years with the following ratios are responsible for the high χ^2 value:

1861......	7.5% silver	24% cross	68.5% red	280 pelts
1868......	18.2% silver	36.9% cross	45.9% red	375 pelts

If these are omitted from the data the χ^2 falls to 5.56, a value that is quite probable in such fluctuating data. At the same time the heterogeneity value falls to 6.66, which is not significant. Thus all years with the exception of 1861 and 1868 can be explained by the single factor hypothesis.

A full explanation of these two discrepancies can be given only when and if historical material becomes available for this section. Both of these years were peak years for white fox so two theories can be advanced to explain these exceptions. First, in each of these years the fur was not drawn from the whole area normally covered by the post; the presence of large numbers of white fox induced trappers to go to coastal and barren land regions instead of inland. Since the topography of this area is conducive to the formation of pockets with different gene frequencies, then the omission of some pockets with different gene frequencies would distort the ratio. That there are such pockets in this area will be shown when we analyze the recent data. Second, migration into this area of southern type foxes may have distorted the ratio.

Forts Good Hope and Norman have similar phenotypic ratios and may be considered together. Testing total data for single factor inheritance we get a very poor fit. If we split the data up into groups of more constant ratios we get the following χ^2's:

$$
\begin{array}{ll}
1861-70\ldots\ldots\ldots & 38.9 \text{ (omitting 1861 and 1869) } 6.6 \\
1871-80\ldots\ldots\ldots & 0.30 \\
1881-93\ldots\ldots\ldots & 4.94
\end{array}
$$

These results are similar to those at Fort McPherson in that with the exception of two years all ratios can be explained by the single factor inheritance. It is interesting to note that one exceptional year is the same in both cases, while the other exception consists of two following years 1868 and 1869.

Fort Providence is situated at the point where the waters of Great Slave Lake pour into the Mackenzie River. It should be little influenced by foxes

from the barren lands but would be one of the first posts reached by a migration from the good fox country to the south.   Testing the total 1860 data for single factor inheritance we get a χ^2 of 22.9.   Plotting the data we find some very erratic changes in the ratio that may account in part for the large χ^2.   After dividing them into fairly homogeneous groups we get the percentages silver and cross, the yearly mean number of pelts, and the χ^2 given in Table I.

TABLE I

COLOUR PHASE DISTRIBUTION OF PELTS TAKEN AT FT. PROVIDENCE

	Silver, %	Cross, %	Mean no. pelts	χ^2
1862–69	14.4	34.6	34	21.6
1862–69 (omitting 1863, 1864, and 1867)	9.2	36.3	31	1.71
1863, 64, and 67	23.0	26.5	38	66.4
1870–78	12.1	40.2	38	4.3
1879–81	8.7	26.2	27	13.5
1882–84	7.6	47.3	66	3.2
1885–93	6.6	32.2	63	6.1

From this table we find that there are six years that are not compatible with the single factor scheme.   The first grouping of 1862–69 gave a large χ^2 of 21.6 and a very large heterogeneity χ^2 of 43.35 with 7 degrees of freedom. The three years 1863, 1864, and 1867 account for most of the discrepancy and when they are subtracted the chi square drops to 1.71 with no significant heterogeneity.

The years 1879–81 do not fit the single factor ratio and form a homogeneous group.   Both groups are characterized by low percentages of cross fox and the first group has an exceptionally high percentage of silvers.   No explanation for these exceptional years will be advanced until we have examined the collections from the surrounding posts.

The relation between the percentage cross and the total foxes at this post is a varied one.   In the 1864 population low the percentage cross is at its lowest point.   At the 1872 low the percentage cross reaches one of its highest points and is consistently high all through the seven years of the population low.   In the 1880 low the crosses again become very scarce, but in the last two years of this low the crosses become more numerous and reach their highest percentage one year before the population peak.   There seems to be no correlation either positive or negative between population peaks and the percentage cross in this case.

Fort Resolution lies on the south shore of Great Slave Lake.   Unfortunately the early data only go from 1862 to 1877.   When the data are examined it is found that two years, 1866 and 1870, have exceptionally low percentages of

cross fox and high percentages of silver.   If we omit these two years and then divide the data into four groups we get the following results:

	Silver	Cross	Mean	χ^2
1862–71 (minus 1866 and 1870)	7.7	34.3	66	5.3
1866 and 1870	14.8	23.2	91	38.4
1872, 1876, 1877	7.9	38.7	136	0.3
1873–75	13.0	29.4	77	28.7

From these figures it would appear that the first 10 years, with the exception of 1866 and 1870, could be explained by the single factor inheritance.   The second period of six years with a chi square of 13.0 is not explainable by single factor inheritance.   It has too many silvers.   Splitting it into two groups of three years each we find that the years of low silver percentage are explainable by the single factor theory, whilst the other three years (1873, 1874, and 1875) have too many silvers and too few crosses to fit into this scheme.

Fort Rae on the north arm of Great Slave Lake is greatly influenced by conditions in the barren lands.   The ratios fluctuate a great deal and it is necessary to make groups of only two or three years in order to keep the data homogeneous.   The tests for fit to a single factor scheme are given in Table II.

<div align="center">TABLE II</div>

<div align="center">COLOUR PHASE DISTRIBUTION AND YEARLY PELT NUMBERS AT FORT RAE</div>

	Silver, %	Cross, %	Mean no. pelts	χ^2
1862–68	7.5	36.3	207	3.4
1869–70	11.1	34.2	152	12.7
1871–75	7.4	30.0	256	40.7
1876–78	9.8	39.3	154	1.8
1879–80	12.7	29.2	106	17.5
1881–83	8.0	35.4	71	1.3
1884–85	13.1	29.7	133	39.2
1886–87	7.5	27.5	140	12.6
1888–90	6 2	35.7	75	0.3
1891–93	13.7	38.0	32	3.4

From this table we find that there are 19 years whose ratios could be explained by a single gene and 13 whose ratios cannot be so explained.   The years that are not fitted by the single factor hypothesis lie in two main groups, 1869–1875 and 1884–1887.   Each of these periods is started by two years of very high percentage of silver.   We find that these nonconforming years with a high percentage of silver can be grouped as follows:

<div align="center">

1869 and 1870. . . . .   11.3% silver
1879 and 1880. . . . .   13.3%   "
1884 and 1885. . . . .   13.3%   "

</div>

It is interesting to note that the years of abundance in the white fox population were 1869, 1878, and 1884. The three high silver exceptions came when foxes had peaked and were migrating south from the barren lands. Thus it appears that the extra admixture of northern blood may be responsible for the distortion of the coat colour ratios.

Inspection of the table shows also that years when less than 100 pelts were taken fit the single factor theory. In such years it is probable that all foxes taken are local stock and that the indigenous population at this time contained only one main coat colour gene. At the times of high populations outside this area we get a migration into the area of either northern type fox or southern type fox. Each of these types have a different ratio and either may possess another coat colour gene at a different locus or of a multiple allelomorphic series.

In view of the small population numbers involved and the lack of historical information about the collecting activities of the posts at this time, it does not seem advisable to formulate any elaborate theory to explain these discrepancies. Inbreeding with its concomitant increase in homozygosity could account for two of the exceptions but not the others, which show a significant increase in silvers with no accompanying decrease in cross fox. Random fluctuations in such a small partially isolated population undoubtedly account for many of the fluctuations but there are enough residuals to lead us to suggest an alternate explanation. If we regard these figures as a true sample of the population (a point open to dispute in these older data) then we must postulate selection of a fluctuating type or migrations from an area of different gene frequency with the migrants probably carrying the Canadian mutant silver gene.

Turning next to the Fort Simpson, Liard, and Nelson series, we find that the yearly numbers are very small. Also, the inaccessibility of the country makes the discarding or local utilization of inexpensive pelts more likely. At Fort Simpson there are always a few more silver pelts than would be expected under the single factor hypothesis, yet no particular year or pentad accounts for this difference. The χ^2 tests by pentads are consistent with a single factor hypothesis, yet the χ^2 (15.48) for the total indicates a very bad fit. The test of heterogeneity reveals that the data are homogeneous, so the disparity in the total ratio seems to be due to the accumulation of all these small excesses of silver. Forts Liard and Nelson show the same condition of a slight cumulative excess of silvers.

The population data reveals neither sharp fluctuations nor cycles. The trapping pressure was probably very low since there were great numbers of more valuable and less bulky furs available in this region at this time. Since populations of fox in this region are more isolated and exist in smaller numbers than in the rest of the range, the possibility of inbreeding with increasing homozygosity was investigated. The homozygosity varied from .64 to .67 but showed no evidence of a distinct trend so migration must be enough to counteract the isolation.

Genetics of the 1915-45 Series

Before attempting to analyze the recent figures it is necessary to know a little more of the history of Fort McPherson. In the period 1860–85, Fort McPherson with its outpost, Pierres' House, was collecting from a large area comprising the Mackenzie Delta, the Porcupine watershed, and North coast of Yukon and the Arctic coast to Baillie Island. Before the recent data start, Fort McPherson area had been divided up among the following posts: Arctic Red River, Aklavik, Hershel Island, and Kittigazuit. During the 1915–45 period, Hershel Island and Kittigazuit were closed out, and Tuktuk and Coppermine opened up.

Evidence that the gene frequency is not the same all through the region, at least not in recent times, is presented in Table III.

TABLE III

PELTS COLLECTED FROM 1915–44

———	Silver	Cross	Red	Total pelts	Yearly average	χ^2
Fort McPherson	.0523	.377	.571	2483	83	2.6
Aklavik	.0302	.326	.642	9569	330	69.2
Arctic Red River	.060	.391	.549	4019	134	1.18
Kittigazuit	.072	.398	.530	501	42	0.03
Tuktuk	.0298	.380	.592	2878	262	37.47
Coppermine	.0257	.275	.700	5172	270	0.62
Hershel Island	.036	.330	.632	1303	77	0.91
Good Hope and Norman	.043	.348	.609	8472	326	3.60

The percentage silver varies from 2.5 to 7.2, cross from 27.5 to 39.8, and red from 53.0 to 70.0. From the χ^2's in the last column of Table III we see that all posts with the exception of Aklavik and Tuktuk fall into the single factor theory.

Aklavik and Tuktuk are adjacent posts. The yearly collections at Aklavik have been influenced by the opening and closing of surrounding posts. Hershel Island closed in 1933, Kittigazuit closed in 1928. Tuktuk did not open until 1935. The collection from 1915–30 was presumably obtained in the immediate vicinity owing to the operation of these other posts. The average yearly collection for this period was 116 compared to 455 for the next 15 years. Testing the first 15 years we get a χ^2 of 4.68 so this earlier period is compatible with the single factor interpretation. In the period 1930–1945, the first 10 years are characterized by too high a percentage of cross and too low a percentage of silver.

The only years that fit a single factor hypothesis are 1931, 1935, 1936, and 1937. The χ^2 for each of the other years is much too high. In the period 1942–1946 the χ^2's are compatible with a single factor interpretation but the

heterogeneity factor is significantly high. There is a definite trend in both the percentage cross and red, the lines of best fit being:

$$\text{Cross} \dotfill \quad Y = 20.8 + 1.058 \, X$$
$$\text{Red} \dotfill \quad Y = 69.77 - .620 \, X$$

In the years 1922–42 the crosses were increasing at the rate of slightly over 1% per year. The past five years have not been on this line and it is too soon to say whether this represents a change in trend or merely a chance fluctuation from the previous trend. The percentage of red shows a decrease of 0.62% per year in the period 1922–42. This decrease in reds is noteworthy since it is opposite to the general trend for the region. When the fluctuations of the reds are plotted about the trend line they tend to show a cyclic tendency with 4, 6, 5, and 4 years between consecutive peaks. The crosses show a less regular cyclic tendency.

At Tuktuk, which opened in 1935, all years except 1937 and 1942 fit the single factor hypothesis when tested separately but there is too much heterogeneity in the 12-year composite figure to get even a remote fit. No trend is evidenced in these data but there is a cycle in the reds with peaks in 1935, 1939, and 1944. The significant point about these peak percentages of reds is that they all occur at population minima.

At McPherson and Arctic Red River the trend in red fox percentages is less than at Aklavik and in the opposite direction the equations being:

$$\text{McPherson} \dotfill \quad Y = 55.6 + .130 \, X$$
$$\text{Arctic Red River} \dotfill \quad Y = 44.0 + .571 \, X$$

It will be noted that these trends that have their origin at 1915 will come to the same percentage reds in 28 years. The red data for the two posts for the past seven years are identical. The percentage cross also shows a negative instead of a positive slope as in the Aklavik data.

The equations for the cross fox are:

$$\text{McPherson} \dotfill \quad Y = 38.24 - .064 \, X$$
$$\text{Arctic Red River} \dotfill \quad Y = 46.50 - .391 \, X$$

The slope in the McPherson data is very small and reveals little change in either the cross or the reds.

Examining the recent series for Fort Good Hope and Norman, we find there is a distinct break in 1930. Prior to that time the silvers averaged 6.0% and after that date they dropped to 2.5%. There was no change in the cross percentages. Grouping the data for each of the two periods we get a χ^2 of 0.08 for 1915–30 and a χ^2 of 46.0 for 1931–46. There is evidently some discrepancy in the data of the second period, which causes us to use other methods of analysis. The difference between the sum of the χ^2's and the χ^2 of the sum is not significant, therefore the data are not heterogeneous. Furthermore, the χ^2 for the individual years are very low and indicate no significant departure from the single factor hypothesis except in 1930 and 1934. The reason for the lack of fit in the 1930–46 data is the shortage in the percentage

of silver. This scarcity of silvers is not enough in any one year to cause a significant departure from the expected, but the accumulation of these shortages causes a very significant departure in the grouped data.

Examining the recent series for Forts Good Hope and Norman, we find that while the pelt figures show a well-developed 10-year cycle that fluctuated from 100 pelts per year in lows to 600 pelts per year in highs, there is no upward trend. The last low, however, is twice the magnitude of the preceding ones.

The colour ratios in toto and by years are compatible with a single factor interpretation. There is a trend in the percentage of reds that gives an average increase of 0.35% per year. The interesting point about these percentages is that they exhibit a four-year cycle that is independent of the 10-year population cycle. Further study of the highs in percentage of reds shows that they correspond roughly with the arctic four-year cycle. The estimation of the number of migrants that may have come into the section and influenced the ratios is complicated by the fact that such migrants fall into two classes; those that come into the region in the fall and are trapped the succeeding winter before they have a chance to influence the genetic composition of the indigenous stock, and those that become established in the breeding population. These latter migrants do not affect the ratio until the year after immigration when their gene frequency is superimposed on the population and leads it to seek a new equilibrium.

In Fig. 5 is plotted the pelt numbers and percentage red phase for the fox taken at these two posts. The trend in reds and the population cycle are quite obvious. In order to get some indication of the possible number of migrants the population figures have been smoothed to the 10-year cycle. The shaded area lying between the frequency polygon of pelts actually taken and the smoothed 10-year cycle is taken to give a rough indication of the number of migrants. Supporting evidence that migrants may come into the area is found in the secondary cycles the peaks of which show up in 1921, 1931, 1940, etc.

Assuming that these proportions of migrants are reasonable estimates of the number of migrant pelts in the collection, we can use these values for the basis for further calculations. For instance, in 1931 there were 60 native fox and 96 migrants, and, in 1932, 51 natives and 50 migrants. These migrants must have come from the north (the only area with excess population in that vicinity at that time) and would have colour ratios typical of the northern stock. The ratio for the indigenous population was 6% silver, 34% cross, and 60% red, which is fairly close to the expected for a single factor at equilibrium. The ratio for northern stocks was 3% silver, 38% cross, and 59% red, which is not a single factor equilibrium ratio. The actual numbers and expected numbers if all pelts came from the indigenous stock would be:

	Silver	Cross	Red
Actual..........	9	96	152
Expected........	15	87	155

$$\chi^2 = 3.34$$

This is close enough to expectation that no other explanation need be sought but the constant bias of too few silvers and too many cross makes another explanation desirable especially since the χ^2 of the total gives a significant difference. Assuming that the proportion of natives and migrants is as stated stated above, then using the appropriate ratios we get the following:

	Silver	Cross	Red
Actual..........	9	96	152
Expected........	11	93	153

The fit obtained by this method is much closer than that obtained in the absence of migrants. However, since two assumptions must be made (i.e. number and colour ratio of migrants) before calculations can be performed, the extensive use of this method is problematical. A further complication is that this method makes no allowance for the migrant individuals that stay and breed thus adding their offspring to the colour phases of pelts found in future generations.

Confirmatory evidence for this hypothesis of migration is obtained from an examination of Fig. 5. It will be seen from this graph that each peak in the percentage of reds corresponds to a shaded area of the population cycle. In other words, a probable migration into the region causes upsurge in the percentage reds. This statement is important as it provides evidence against the selective force of mere population numbers developed and analyzed thoroughly by Calhoun (3).

In view of this migration hypothesis it is necessary to go back over the data already presented and re-examine it. Before doing this it is necessary to clear up one point. The $p^2 : 2pq : q^2$ formula used as the criterion of the presence of one or more coat colour genes is based on the equilibrium condition in an extensive population (Wright (9–12)). We have been using it for small partially isolated populations where it only holds when migration, mutation, and selection are of a certain magnitude. We have assumed that mutation is negligible and need not be considered. Migration in most cases has been considered just sufficient to prevent inbreeding, while the role of selection has not been considered so far.

When we analyzed the data for Aklavik, we found a very evident decreasing trend in the reds and that all but seven years were compatible with a single factor interpretation. These seven years do not fit into a two factor arrangement either, so in view of the fact that the other coat colour alleles were not present at Fort Good Hope and Norman, it seems advisable to postulate migration in this case also.

In Fig. 4 are plotted the population numbers and gene frequency of the red pelt-producing allele (assuming single factor inheritance) for Arctic Red River and its adjacent post Aklavik. The opposing trends in gene frequency are plainly seen in this graph. Prior to 1930 population numbers were small,

gene frequency fluctuations violent, and the two populations far apart in their gene frequencies as can be seen by the following example.

1925
            Aklavik................. 25% cross, 73% red.
            Arctic Red River......... 42% cross, 47% red.

After 1930 there was a sudden upsurge of population especially at Aklavik and the gene frequencies at the two posts became almost identical.   This can be clearly seen from Fig. 4.   The color ratios in 1936 were identical, both being:

40% cross, 56% red.

From the trend of these gene frequencies it is plausible to suggest that the upward trend of red foxes at Arctic Red River and the downward trend at Aklavik are due to the mixing of the two sets of frequencies by migration in both directions.   If this is the case, then we should expect that in some years three classes of fox would be present and equilibrium ratios would not be obtained.

Fort McPherson data are intermediate between those at Aklavik and Arctic Red River throughout the 27 years.   Since there is no pronounced increase in the population at this point, it seems that there has been no increase in the movement of animals to or from this section.   The Fort McPherson collecting area probably includes part of the gene frequency range of Aklavik and Arctic Red River since it is situated between them.

At Tuktuk the heterogeneity is probably due to similar migrational movements with the possible complications from the four-year arctic cycle.   The high percentage of reds that occur at population minima are of the typical western arctic type.   Coppermine, farther to the east, had 70% red compared with Tuktuk's 59% red (see Table III).   The population at Coppermine, Bathurst Inlet, and other Western Arctic points does not seem to reach equilibrium gene frequencies.   The yearly collections are so small that the chance deviations obscure any trends due to migration or selection.

At Fort Simpson, which lies at the junction of the Mackenzie and Liard Rivers, we find that the percentage of red and cross fluctuates with the population.   Reds show a correlation of $+.32$ and cross show an inverse relationship.   There is a definite cycle in both the cross and the red figures but there is no upward or downward trend similar to that observed in the population figures.   The only abnormality observed is that in the last peak the reds did not increase or the cross decrease as quickly as expected.   Testing these data for single factor inheritance, we find that there are two periods that will not fit.   These are 1924–1928 and 1938–1945.   The first is a population peak with the precentage silver too high and the second occurs when the cross and red percentages reacted abnormally and the percentage silver was too low.

Both of these abnormalities can be explained best by migration.   In 1924–28 migration from the adjoining Providence area would affect the ratio as follows:

				Silver	Cross	Red
700	Native	6.0S; 31C; 63R	=	42	217	440
627	Migrants	1.7S; 20.3C; 78R	=	11	127	490
1327	Pelts	4.0S; 26C; 70R	=	53	344	930
1327	Actual pelts	4.0S; 25C; 71R	=	54	335	938

Similar explanations can be worked for other nonconforming ratios. Imposed on this simple picture will be the complications arising from the migrants that stay and breed.

Forts Liard and Nelson lie southwest of the other posts and their collecting area is more or less confined by mountain ranges. The country does not provide good habitats for fox, consequently the collections are always small. The population is cyclic with a very pronounced trend, each succeeding peak being 40 to 100% higher than. the preceding one. There is also a definite trend in both the cross and red percentages, the straight line relationship being:

$$\text{Cross} \ldots \ldots \quad Y = 43.4 - .484\,X$$
$$\text{Red} \ldots \ldots \quad Y = 50.3 + .553\,X$$

From these equations we see that reds are increasing at a slightly faster rate than cross are decreasing; the difference is made up by the decrease in silvers. Besides the trend line there is also a cyclic movement of reds and crosses. When the population increases the percentage red also increases and the cross decreases.

Testing for monofactorial inheritance we find no significant departure from the expected. All yearly and total pelt numbers could be explained on the basis of a single factor; the increase in population and increase in percentage red being due to immigration from areas of different gene frequency.

At Providence and Hay River, which draw their furs from the vicinity of the western end of Great Slave Lake, we find that only part of the yearly data are fitted by the single factor hypothesis. The population here is cyclic and the ratios obtained at the peaks will not fit whereas those obtained in the troughs will fit. These posts collect a lower percentage of cross than any other post so far encountered. In population highs the discrepancy in single factor ratios arises from too high a percentage of silvers in proportion to the crosses. Both red and cross percentages have cyclic fluctuations similar to the general population. For the first two cycles, the percentage of reds increases along with the population and reaches its peak just prior to the population peak (Fig. 6). From 1938–46 this relationship no longer holds. The reds seem stabilized at a higher level until 1943 and then decrease while the population is still increasing. The cross percentage shows the opposite relationship for the first two population cycles. It increases when pelt numbers decrease and reaches its peak at the population low. Since 1937, it has also been irregular and the opposite relationship seems to hold.

Fort Resolution lies on the south shore of Great Slave Lake and draws most of its collection from the south and east end of the lake. It is nearest to the good fox country of Northern Alberta and Saskatchewan and therefore most likely to be influenced by a migratory influx. The population graph (Fig. 7) shows a typical 10-year cycle with increasing peaks. The percentage of reds shows what appears to be a four- to six-year cycle about a decreasing trend of $Y = 78.5 - 0.269 X$. The ratios prevailing during the first and second population lows and the last high are consistent with the single factor theory but the other ratios are not.

At Fort Rae, on the north arm of Great Slave Lake, we find that the population again exhibits a clear-cut cycle with no trend. The only noteworthy departure from the normal rhythm is that the collections in the last low are two to three times greater than in previous lows. In Table IV the data are grouped by years having more or less the same proportion of silvers, cross, and reds. It is apparent from the χ^2 column that only in the past three years could the ratios be explained by the single factor theory. The percentage of reds again shows a direct correlation with population changes. The magnitude of the variations in percentage of red in the earlier years is much greater than at any other posts. This can be seen quite clearly by comparing Fig. 8 with Fig. 7; the same scale is used in each.

It is apparent from the χ^2 in Table IV that the deviations from a single factor ratio are much larger than would be expected by chance, and that

TABLE IV

COLOUR PHASE DISTRIBUTION OF PELTS COLLECTED AT FORT RAE

	Silver, %	Cross, %	Mean	χ^2	n	q
1916–22	3.46	23.7	154	11.3	.14	.125
1923–26	2.32	14.8	488	52.6	.082	.127
1927–33	3.96	23.7	212	30.0	.14	.150
1934–36	2.24	17.7	610	40.1	.095	.148
1937–42	2.77	21.3	325	16.1	.124	.105
1943–45	1.48	22.3	495	0.2	0	.127

some other explanation will have to be sought. The one lone exception is the period 1943–1945. It is also apparent that the two lows and the two highs have very similar ratios as can be seen below:

	Lows		Highs	
Silver...............	3.5	4.0	2.3	2.2
Cross................	23.7	23.7	14.8	17.8

The irregular nature of the fluctuations over the last eight years is shown in their nonconforming ratios. The percentage of silver is the same as for the highs, and the percentage of cross is similar to the lows.

From the differences in the ratios between the highs and the lows we deduce that the composition of the population is not the same in periods of population abundance as it is in times of scarcity. When fox numbers are low, the foxes taken are apt to be of local stock and represent the typical ratio for that district.

When the population begins to increase, it is aided by migration from other sections of the country. There is evidence that the cycle in foxes does not reach its peak in all parts of the country at the same time. The first upswing in population cycle comes in the Lake Athabaska and Peace River area and spreads north, south, and east from here. The Rockies form a partial boundary to the west and the British Columbia cycle seems independent. As supporting evidence for this point, the times of the peaks of the 1934–36 cycle can be quoted. The peak year was 1934 in the Athabaska and Peace River area, 1935 in the Resolution, Rae, Providence, and Simpson areas and parts of British Columbia. By 1936 it had spread to the rest of British Columbia and the delta of the Mackenzie. Other peaks show a similar consecutive order although the lag is not always the same.

A corollary theory is that the gene or genes concerned with coat colour also influence the propagative or survival ability of their carriers. Thus, at Fort Rae, in times of fox population scarcity when interspecific strife is low and cubs are better cared for, the silver-producing gene is favored and a higher percentage of silvers are raised to trapping age. In times of abundance the interspecific strife is higher and the silvers are less favored and a greater percentage of reds is produced. If such were the case the percentage of cross would show proportionate increases and decreases in the following year.

Applying the dihybrid interpretation of Warwick and Hanson (1) and using the formula suggested by Calhoun as a simplification and extension of Butler (2) we get the series of figures in the last two columns of Table IV. The formulae suggested by Calhoun are:—

$$n = \frac{C}{C + 2R}$$

$$q = \frac{m^2 - R}{m^2}$$

C = frequency cross, R = frequency reds

$n + m = 1$ = frequencies of Alaskan gene A/a

$p + q = 1$ = frequencies of Canadian gene B/b

It will be seen from Table IV that during the first two peaks there was a regular relationship between the population highs and lows, Column 3, and the frequency n, Column 5, of gene a. While the frequency q of gene b increased steadily the frequency n has fluctuated being highest (0.14) at times of population lows and smallest (0.082 to 0.095) at times of population highs. In the 1937–43 low, the percentage silver and cross did not get as large as in past lows and so neither frequency n or q is as high. However,

n does show a considerable increase, from 0.095 to 0.124 over the previous peak. In the final peak, 1943–45, a different situation arises. In 1943, at points to the south, red foxes had reached their highest peak in history, while from the northeast there was a southern migration after a peak the previous year at Bathurst Inlet. Partly because of this southern migration and partly from lack of food (rabbits were decreasing around Great Slave Lake in 1943), the spread of the southern population seems to have been directed eastward over the prairie park lands and northwestward down the Mackenzie. Because of these facts, the peak collection at Fort Rae did not rise as high as previous peaks whereas at more southerly points the peak was 50 to 100% higher than any previous one. Accompanying this population phenomena, we find that there are no longer two recessive genes present in the population. The ratio can be explained by one gene with a frequency of 0.127.

These changes in gene frequency are explained more easily by migration than by selection. When the population increases it is chiefly because of the emigration from the south. Such foxes are characterized by the low frequency (n) of gene a. Influxes of foxes of this type cause n to drop whenever the population increases. Little can be said about the magnitude of the fluctuations of n or the relative constancy of q since if the migration hypothesis holds the genes are not in equilibrium and the values of n and q do not depict the true picture. It will be noted that in this case we have postulated two-factor inheritance whereas in other cases we have explained the whole discrepancy by migration. The other cases were tried with Calhoun's formula and either failed to solve or gave inconsistent results. In this case, the discrepancies seem too large to be accounted for by migration so both coat colour genes are considered as being present in the Rae, Resolution, and Providence area.

One of the difficulties in analyzing the results of a single post is that local peculiarities of management are reflected in the ratios. For instance, if the manager pays aggressively for reds and silvers but is not as aggressive in buying cross fox, then these will go to other buyers. Consequently, the resulting ratio will be low in its percentage of cross. We have a check on the Fort Rae data for 11 years in the N.W.T. figures published by Robinson (8). These figures, as can be seen below, show close agreement so Hudson's Bay Company figures can be accepted as indicative of the proportion of various colour phases trapped in the Fort Rae area.

Fort Providence shows the same characteristics as Fort Rae. The percentage of cross is highest (38.7, 20.3, and 24.4) in the population lows and

	Silver		Cross	
—	H.B.C.	N.W.T.	H.B.C.	N.W.T.
1934–1936	2.24	2.29	17.7	18.6
1937–1942	2.77	2.78	21.3	21.4

smallest (19.3 and 16.3) in the peak populations.   Unlike Rae, the ratio can be explained by the monofactorial hypothesis.   The population peaks are of a more abrupt nature than at Rae.   After the initial rise the last peak failed to materialize and the characteristic dip in the percentage of cross does not occur.

At Providence and Hay River, it appears that the population peak is largely due to the influx of immigrants with a higher proportion of the red phase. The correlation between population numbers and percentage red is not close enough for this to be the whole answer.   During the first population cycle the reds increased and decreased with the cycle (see Fig. 6).   In later years, the correlation is either not as marked or is even reversed.   Our interpretation of this is that prior to 1921 most of the indigenous foxes carried only the Alaskan gene.   With the influx of foxes in the first population peak, the Canadian gene was brought in.   Some of these foxes stayed to breed and although partial equilibrium was reached in population lows, each new wave of immigrants changed the gene frequencies.   This would account for the lag between the increase in population and the increase in percentage red.

Examination of the data for Fort Resolution (Fig. 7) reveals that there is no correlation between the percentage of reds and the population cycle.   There is a definite four-year cycle in the percentage of reds that can be explained either by immigration from the north during times of peak abundance or a fluctuating selectivity factor.   It is hard to see how Calhoun's conclusion of gene a being negatively and gene b positively correlated with population size could be applied to these data.   The idea of a cyclic selective force does not seem very plausible but until we acquire a greater knowledge of population cycles and their cause, we cannot disregard it entirely.

Discussion

The presence of the black or silver form of the red fox *Vulpes* sp. has been noted as occurring in the Canadian wild fox populations since the earliest historical records.   Little attention was paid to fox fur at this time so it is lumped with miscellaneous furs; no authentic breakdown by phases is available.

The first records that give the relative abundance of the three phases and the section of country from which the foxes are drawn are those of Elton (6) for Labrador, and Cowan (4) for British Columbia.   These records are both for the 19th century and show that stratification had occurred at that date. Although it appeared that there were concentrations of the silver producing gene in certain areas, it also revealed a definite north/south trend with the proportion of silvers increasing towards the north and decreasing towards the south.   This appears to be a contradiction of Allen's or Gloger's rule of melanin pigmentation within a race.   On the Atlantic and Pacific coasts the proportion of silvers is significantly higher than in the inland districts.

Since 1830 there has been a diminution of the silvers and an increase in the reds.   Accompanying this there has been a rapid increase in fox numbers in recent years, especially in the centre of the range.

The percentage of each of the colour phases present varies with the locality and a definite cline is shown.   Silver and cross are more abundant in the north than in the south and show a steady decrease as one moves southward.   An exception to this is in the Liard valley.   The silvers and cross increase as one moves southward up this valley from Fort Simpson to Fort Nelson and then the normal north/south cline is established for the rest of British Columbia. The percentages of silver and cross also vary with time, there being a large decrease in percentage of silvers and crosses between the 1860 and 1930 periods.

The 1860–1890 data for all posts except Fort Rae can with the exception of a few years be explained by a single pair of alleles.   There are no major trends in population or gene frequencies at this time.   The changes in gene frequency appear to be of the type that could result by chance in a partially isolated breeding population.   Migration from the north balanced out that from the south and also overcame the effects of inbreeding.   At Fort Rae, this does not hold; the ratios appear to be changed by frequent immigration, the migrants bringing in the other pair of coat colour alleles.

In the 1915–46 series, several different trends are visible.   At Aklavik and Resolution the percentage of reds is decreasing while at most other posts it is increasing.   At Simpson, Liard, and Nelson and to a lesser extent at Providence, Hay River, and Rae, the percentage of reds fluctuates directly with the population.   At Resolution, Good Hope, and Norman, the percentage of reds shows a four-year cycle that is not correlated with the 10-year population cycle.   Both these types of gene frequency changes can be explained by migration but they are harder to explain by selection.   This is especially true in the case of the four-year cycle of percentages of reds.

The changes at Aklavik and Arctic Red River would also be hard to explain by selection since the changes are in opposite directions but they can be explained by periodic migrations in both directions from these areas of differing gene frequency.   The mixing has now reached the point where the two areas have practically identical frequencies.   At other points, it was shown that by splitting the population into indigenous and migrant, and then applying the appropriate gene frequencies, a plausible explanation of the prevailing ratios could be obtained.

Points north of Providence are, with the exception of a few years, compatible with the single factor interpretation.   These exceptional years can be explained by migration.   South and east of Providence, the two factor hypothesis seems necessary.   At these latter points, there is ample evidence of migration and it is doubtful whether equilibrium ratios are reached.

A provisional working hypothesis of the evolution of coat colour in foxes may be advanced as follows.   The mutation to black occurred in the American red fox sometime prior to 1600.   At least two different gene mutations occurred, one in Labrador and one in British Columbia or Alaska.   The fox population was small enough at this time that the recurrent mutations found themselves in a population that had become divided into small, partially isolated groups.   Under these circumstances, differential population growth

and migration made possible the establishment of the mutation and their distribution throughout the country. It may be significant to note that these mutations arose in poor fox habitats.

The two mutations are genetically different and now overlap over most of the foxes' range. The huge increases in population have taken place mostly in Alberta and Saskatchewan where the density of the silver producing gene is lowest, thus most migrants come from areas of low silver density. The increase in this region is due not to the adaptive ability of the local fox type but to the sudden changes in its habitat, such as settlement in Peace River and other northern areas.

In these small partially isolated groups the frequencies of the coat colour genes drift back and forth irregularly and might reach fixation because of the inbreeding that occurs in small populations. The local race, however, is subject to a small amount of cross-breeding with the rest of the species and the tendency towards fixation is balanced by immigration pressure instead of mutation and selection. North-south migrations would establish a cline since a greater proportion of migrants would stay and breed in adjacent areas than in distant areas. If local selection is stronger than migration pressure, well defined local races would arise.

No allowance has been made for an admixture of European red fox genes. We know that the English red fox, which lacks the coat colour mutation, was imported into the New England States for fox hunting and is presumed to have spread west and north. These genes may now be present in southern Ontario but certainly are not in the area under discussion.

We have assumed that the silver-producing gene is indifferent to selection but there is little critical evidence on this point. It is obvious that under domestication silvers can be raised as easily as reds. This cannot be due merely to the selection of the proper genetic background because outcrosses to wild stock do not affect the fecundity or viability of the silver segregants. No significant differences between red and silver litter sizes have been observed. Nothing is known about the differences in foraging ability, or predator relationships between the various colour phases, but it is often inferred that man, the arch-predator, is discriminatory (Elton (6), Haldane (7)).

One of the big problems in constructing an evolutionary theory that will hold for fox populations is the constant flux in population density. Short time oscillations in population numbers cause minor changes in gene frequency (Wright (11)). In cyclic lows the population is reduced to a few individuals with restricted range and a large amount of inbreeding. At such times there is a fixation of genes at the rate of $\frac{1}{4N}$ per generation where N = the new population number (Wright (12)). In population highs the breeding is random in areas of high density. With high density and concomitant overflow or migration to surrounding areas, at least three things may happen to the mig-

rating foxes.   (1). They may find the population of the adjacent area still relatively sparse and they could find vacant habitats in which to stay and breed both among themselves and with the indigenous population.   (2). They may find the neighboring population also reaching its peak and any foxes that stay would be forced to take marginal habitats.   This would decrease their chances of breeding and raising successful litters.   (3). They might find the neighboring fox also at peak population and the migrants would be forced to pass right on through this territory.   Needless to say, each of these conditions would affect the fur catch and colour ratio differently.

The colour phase ratio of the population would be affected two ways by immigration.   If the migrants carried the same alleles as the indigenous population, there would be a more or less mechanical mixing of the two gene frequencies, and the percentage of cross and silver would increase or decrease together.   If the migrants carried a different pair of coat colour alleles then the percentage silver and cross would not vary together.   Both conditions were shown to occur in fox population figures (Butler (2)).

The whole problem of fluctuations and trend in gene frequencies is connected with the cyclic fluctuations and the increasing fox population.   This can be explained by selection (Haldane (7), Calhoun (3)) but a simpler explanation is that of migration following population increase.   Such migration coming from areas of low gene frequency and breaking down the barriers of partial isolation has resulted in a lowering of the gene frequency of the whole population.

The evidence for migration is mostly indirect and comes from the following sources:

1. In the fall of 1942 coloured foxes were extremely abundant at York Factory and relatively scarce at Island Lake 350 miles inland.   After freeze-up the fox became exceedingly scarce at York Factory and abundant at Island Lake.

2. Foxes become abundant every four years in northern Quebec and every nine years in the south of the province.   Consequently at certain times there is a heavy population pressure in the north and a light one in the south.   At such times there is a 'run' of northern foxes, the northern type fur being taken in southern Quebec.

3. In 1943 notes were taken on the abundance of fox in a marshy area with few 'travel-ways'.   The notes indicated a definite seasonal concentration on certain 'travel-ways' and a general exodus from the region.

Acknowledgments

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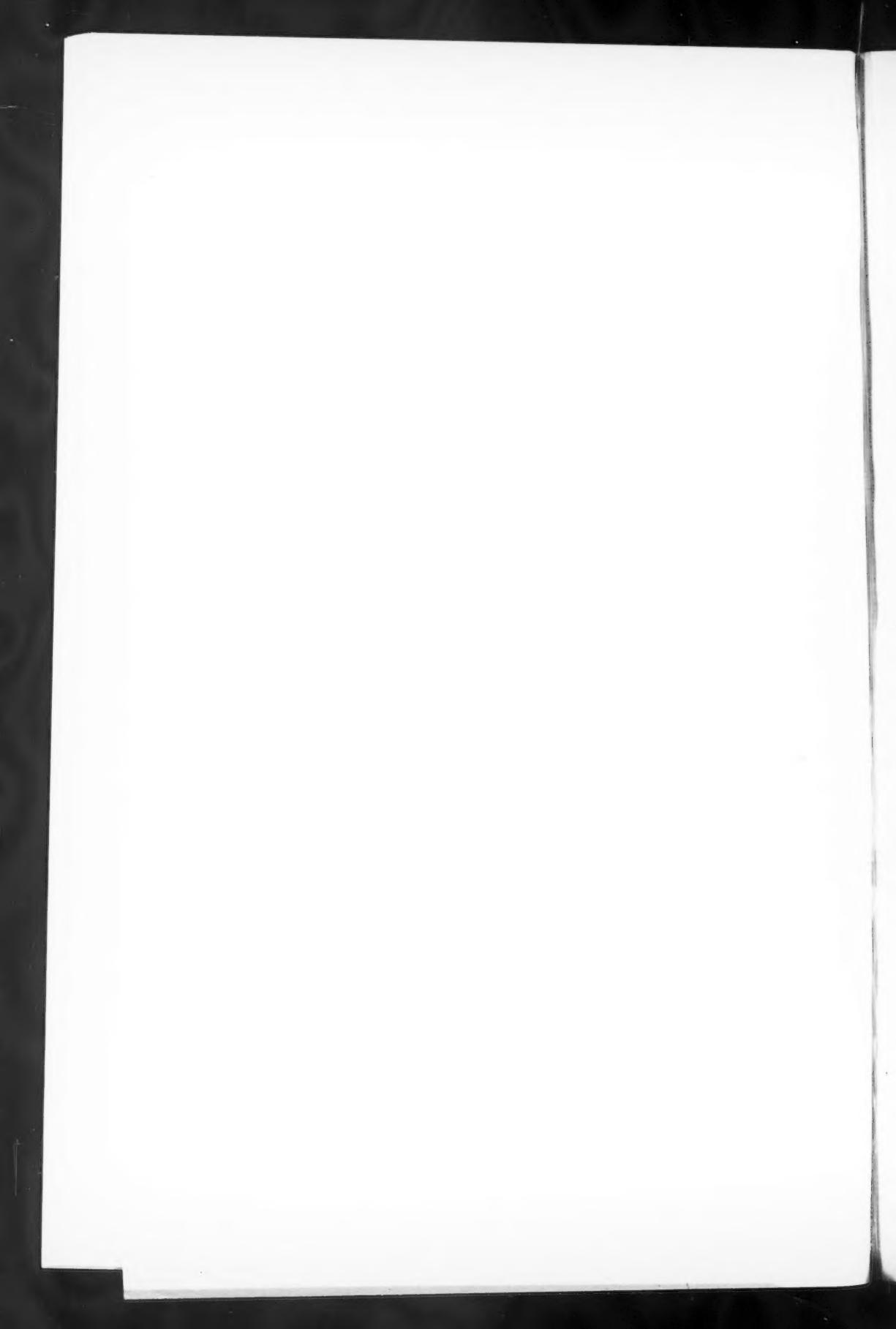
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